

**BODY SIZE AND TERRITORIAL BEHAVIOR IN THE BEE
PROTOXAEA GLORIOSA (FOX)
(HYMENOPTERA: OXAEIDAE)**

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Abstract.—The bee *Protophaea gloriosa* (Fox) exhibits a resource-based mating system with males defending small territories, usually by flowering plants. Males appear to apply scent marks on vegetation near their hovering stations. Male body size is positively correlated with the number of flowers in male territories. Convergent evolution is apparent in the similarities between the behavior of *P. gloriosa* and some other unrelated bees whose males defend foodplants visited by females.

Key Words.—Insecta, mating system, bee territoriality

The large oxaeid bee *Protophaea gloriosa* (Fox) has attracted attention because of its pollination activities and the highly aggressive territorial behavior of its males (Cazier & Linsley 1963, 1974; Linsley & Cazier 1972; Hurd & Linsley 1975, 1976). Territorial males defend an aerial station for several hours each morning. They generally hover within 1 m of the ground near or over a patch of flowers or a shrub. When males are at their stations, they pursue a broad range of moving stimuli and violently drive conspecific males away. Territorial males mate with virgin females that arrive at their hovering sites.

This paper presents new information on several aspects of male behavior, especially on the relation between male body size and the flower-richness of their territories.

METHODS

Work was conducted from 29 Jul–15 Aug 1974 at two locations in desert rangeland approximately 2 and 4 km N of Rodeo, New Mexico. These sites and their flora have been described by Linsley & Cazier (1972: 6) and by Cazier & Linsley (1974: 5). The dominant perennial shrubs, and the focus of male activity at the first site, were *Koeberlinia spinosa* Zuccarini (crown-of-thorns) and *Ephedra trifurca* Torrey (Mormon tea). At the second study site, males of the bee established territories by patches of the annual herb *Kallstroemia grandiflora* Torrey (Mexican poppy).

In 1976, males were observed from 30 Jul–4 Aug in an open pasture at the site 4 km N of Rodeo, where they territorially defended scattered plants of *Apodanthera undulata* Gray, a curcurbit gourd.

In 1989, I watched males of the bee on the mornings of 13–18 Aug at a shrubby field about 3 km E of Portal, Arizona. In this area, males guarded patches of *K. grandiflora*. Counts were made of the number of flowers in the patches patrolled by males. I also counted the number of flowers in the first 20 undefended patches of more than 10 flowers encountered as I walked a straightline transect through the study area.

Super-8 movie films, some taken in slow motion, helped in the analysis of the

behavior of territorial males. In addition, 27 territory defenders were collected in 1976 and later measured as to headwidth with vernier dial calipers accurate to 0.05 mm because headwidth is clearly correlated with body size in this and other bees (e.g., Alcock et al. 1977). The number of *A. undulata* flowers in each male's territory was recorded to examine the correlation between male body size and flower abundance in territories. In 1989, the headwidths of 14 males were measured and data gathered on the number of *K. grandiflora* flowers in their territories.

RESULTS

Plant "Marking" Behavior.—No previous reports on the territorial males of *P. gloriosa* have remarked on a distinctive feature of their behavior, namely the frequent interruptions of hovering that involve a flight to an exposed twig, thorn, stem or clump of leaves on a nearby shrub (commonly *Koeberlinia*, *Ephedra*, or *Acacia*). Once they alight on the plant part, males walk rapidly up the vegetation conspicuously dragging the tip or side of the abdomen against the substrate. As they walk, the mid- and hindlegs first enclose the plant part and then are drawn sharply down and out before returning to their original position (right angles to the bee's body). The bee appears to be embracing and vigorously stroking the plant part (in slow-motion films). The time spent in this activity almost never exceeds a few seconds, although the bee may pause to mandibulate a stem or briefly groom itself.

The frequency of plant-visiting interruptions to hovering flight was 0.37 per min based on 520 min of observation of a total of 22 males watched at *Koeberlinia* in 1974. In 1989 the rate of visits to nearby acacias by 7 males defending *Kallstroemia* patches was also 0.37 per min based on 145 min of observation. Males distribute their "marks" fairly widely within their territories, although they sometimes return to the same spot after a period.

The function of plant "marking" remains elusive, given that I never observed a female (or other male) approaching or landing upon a "marked" site.

Body Size and Territory "Quality."—Hurd & Linsley (1975) noted considerable size variation among males of *P. gloriosa*. If body size is related to competitive ability in this bee, then large males should occupy more attractive sites than small ones. One factor that might affect the quality of a territory is the number of flowers that the male controls.

The males observed in 1976 defended plants of *A. undulata*, which had a variable number of bright yellow flowers at the center of a mass of green leaves covering the ground. Although flowers of *A. undulata* are not visited by pollen- or nectar-seeking females, virgin females may be attracted to the plant; I observed a territorial male copulating with a female on a grass stem a short distance from an *A. undulata*.

Copulation began at 09:26 h on 2 Aug and lasted for 2.3 h during which time the male alternately tapped the lateral surfaces of the female with all three pairs of legs and then paused for a few seconds before repeating the short burst of stroking taps. This pattern persisted until the female departed, after which the male returned to his hovering station a few cm above the central cluster of flowers.

Why virgin females visit *A. undulata* plants that do not offer nectar or pollen is unknown, but in any event a plant's conspicuousness to flying females should

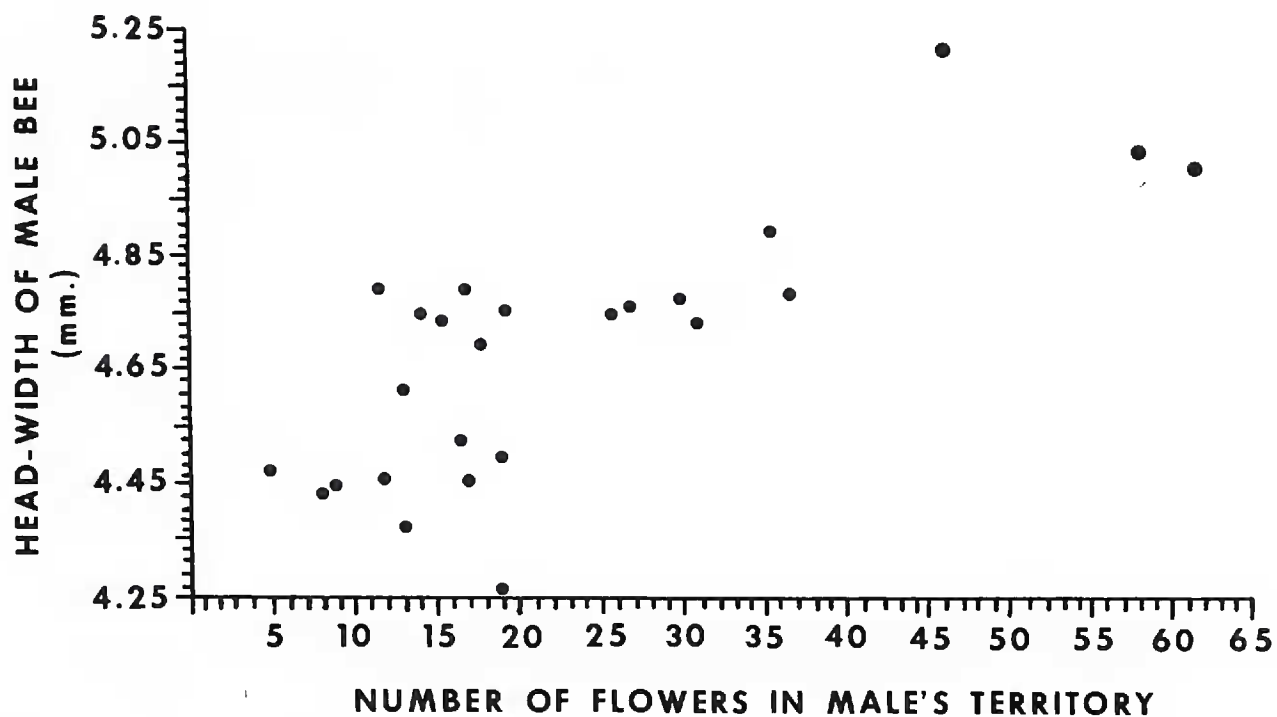


Figure 1. The relation between the headwidths of 27 males of *P. gloriosa* and the number of flowers in bloom on the plant *A. undulata* that they defended.

be correlated with the number of flowers in bloom. The headwidths of territorial males at these plants in 1974 were significantly correlated with the number of flowers in their territories (Fig. 1; $r = 0.65$, $n = 27$, $P < 0.01$).

In 1989, I tested the hypothesis again in an area with patches of flowering *Kallstroemia*, a pollen- and nectar-yielding foodplant for adult males and females of *P. gloriosa* (Cazier & Linsley 1974). Here too the headwidths of territorial males were correlated with the number of flowers that single males monopolized in their defended areas, which were discrete, well-defined patches of *Kallstroemia* ($r = 0.76$, $n = 14$, $P < 0.01$).

The hypothesis that males seek to defend patches with many flowers is supported by the observation that in 1989 hovering males patrolled *Kallstroemia* patches containing a mean of 72.9 ± 53.2 flowers ($n = 14$); in the same field, a sample of undefended poppy patches averaged 33.4 ± 22.2 ($n = 20$, $t = 2.98$, $P < 0.01$).

DISCUSSION

Convergent Evolution and Resource Defense.—Males of *P. gloriosa* exhibit behavioral similarities to many other unrelated bees. Territorial defense of foraging resources by males as a mate-locating system occurs in some andrenids, anthophorids, megachilids and colletids (reviewed in Alcock et al. 1978, Eickwort & Ginsberg 1980). The extent of convergence is illustrated by a comparison of *P. gloriosa* with the small Australian colletid *Hylaeus alcyoneus* Erichson (Alcock & Houston 1987).

In both species some males are territorial at flowering plants visited by many nonreceptive and a few receptive females. It is typical of resource-defending male bees that their females visit well-defined patches of foodplants (Alcock et al. 1978). As a result, individual males can readily identify and economically defend places in the environment that will attract disproportionate numbers of potential mates.

Males of both species are highly scented and while on territory, they leave the flower resources they are defending to "mark" nearby vegetation by rubbing their body over leaves and stems. Although the significance of the "marking" behavior of males of these two species remains to be established definitively, the activity is highly reminiscent to the sex pheromone-marking behavior of certain andrenid bees (Tengö 1979: fig. 3) and carpenter bees (Velthuis & de Camargo 1975, Andersen et al. 1988, Gerling et al. 1989).

Body size influences territorial behavior in both bees with larger individuals more likely to be territory owners in *H. alcyoneus* and larger males more likely to claim flower-rich territories in *P. gloriosa*. Larger individuals enjoy an advantage in aggressive contests in many territorial insect species (Thornhill & Alcock 1983).

Remaining Questions. — There are many unanswered questions on the behavior of *P. gloriosa* (and other bees with resource defense mating systems). First, although some males of *P. gloriosa* defend well defined clumps of flowering food-plants (e.g., *Kallstroemia*), others are territorial at plants whose flowers do not yield usable pollen or nectar (Cazier & Linsley 1963). Still others defend hovering stations by nonflowering shrubs. What is the ecological basis for the occurrence of nonresource-based territoriality in this bee, which is clearly capable of standard resource defense?

Second, what is the advantage of applying scent marks to vegetation (if this is what males of *P. gloriosa* are doing) when the territory usually contains highly conspicuous floral resources that attract females in their own right?

Third, do males of *P. gloriosa* that own flower-rich patches actually mate with more females than those with fewer flowers, an association established only for the resource-defending megachilid *Anthidium manicatum* Linnaeus (Severinghaus et al. 1981)?

Fourth, if large males of *P. gloriosa* hold flower-rich territories by virtue of their fighting advantage, why is there so little evidence for intense competition among males for control of flower-rich territories? In both 1976 and 1989, territories from which males were removed were often left vacant for prolonged periods. Moreover, in 1989 there were many patches of *Kallstroemia* with dozens of flowers that were never claimed during the study, showing that male density was low. Given the availability of undefended flower-rich patches, why did the smaller males in the population choose to defend sites with relatively few flowers?

Fifth, males are larger than their females in some species with resource-defense mating systems (e.g., *H. alcyoneus*) but far from all (e.g., *P. gloriosa*). Sexual selection theory suggests that males should be larger than females in territorial species with intense intrasexual selection for access to mates (Darwin 1871). The basis for the exceptions is unknown, but see O'Neill (1985).

These questions need to be addressed in new studies of resource-based mating systems in bees.

ACKNOWLEDGMENT

I thank Wade Sherbrooke and the staff at the Southwestern Research Station of the American Museum of Natural History. This work was supported in part by National Science Foundation Grant BNS 8620352.

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Received 3 August 1989; accepted 22 February 1990.